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MORPHOLOGY OF KETELEERIA FORTUNEI

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 225

A. H. HUTCHINSON

(WITH PLATES VII AND VIII AND THREE FIGURES)

Since its discovery by FORTUNE, *Keteleeria* has aroused interest as an endemic Chinese conifer. It was found first near the temple of Foo Chow Foo, and reports of recent explorers locate it near ancient shrines. Whether *Keteleeria*, as seems most probable in the case of *Ginkgo*, was a sacred tree and has been preserved by a religious order is a matter of conjecture.

Because of limited knowledge, even of the gross structure and characteristics, it is not surprising that the form now known as *Keteleeria* has been variously placed by systematists. LINDLEY named this form *Abies jezoensis*, mistaking it for a Japanese species of that name (14). MURRAY, in 1862, showed that the form in question differed from *Abies jezoensis* and called it *Abies Fortunei* after the original discoverer. In 1868 CARRIERE made a new genus *Keteleeria*, naming it after KETELEER, a Belgian horticulturist. PARLATORE placed the same form under the genus *Pinus*, as *P. Fortunei;* by BENTHAM and HOOKER it was classified with *Tsuga;* BENTHAM and MASTERS again placed it in the genus *Abies;* while by ENGLER it is described under *Abies*.

CARRIÈRE'S reasons for making a new genus were that the form in question differs from *Picea*, since it has erect cones; it cannot be included with *Abies* because the cone scales are persistent; and at the same time, in habit and general aspect it resembles *Podocarpus*. Further, PIROTTA (14) states that a new genus is justified because of the arrangement of the staminate strobili ("fiori maschili"). The bud of the staminate strobili is borne either in the axils of the leaves of the preceding year or at the apex of a branch. PIROTTA regards the cone clusters as true "inflorescences." Each "inflorescence" consists of a short peduncle dilated at the apex into a receptacle-like body which is invested by scales; the lower scales are short, those above becoming increasingly longer. The "flowers" are situated on the margin of the dilated peduncle in the form of a circle or false crown, one or two "flowers" being situated near the center of the receptacle. The number of staminate cones in a cluster ranges from 6 to 10. It is rather remarkable that the other genus of Abietineae (*Pseudolarix*) which shows such an arrangement of staminate cones is also an endemic of China. PIROTTA regards this character of sufficient importance to warrant the division of Abietineae into the Euabietineae, including those forms whose staminate strobili are single (*Abies*, *Picea*, *Pseudotsuga*, *Tsuga*), and the Pseudoabietineae, including those forms whose staminate strobili are in clusters (*Keteleeria* and *Pseudolarix*).

PIROTTA (15) has examined also the anatomical structure of the root, stem, and leaves. The root is characterized by a primary axial resin canal, by secondary canals arranged irregularly in the secondary wood, and by the presence of resin-bearing "idioblasts" in the secondary cortex. In the branches there are resin canals and mucilage-bearing "idioblasts" in the primary cortex only. The leaves are bilateral and contain 2 marginal resin canals and also mucilage "idioblasts" in the mesophyll.

The vascular anatomy has been studied also by HOLDEN (11), who says "*Keteleeria* has the wood structure of *Abies*. Ray tracheids are entirely absent even in such primitive structures as the first annular ring, cone-bearing branches, cone axis, and are not recalled after wounding, although there is an abundant formation of traumatic resin canals."

RADAIS (17) has classified conifers according to the distribution of the resin ducts ("caneau sécréteurs") in the megasporophylls. Upon this basis *Keteleeria* is placed with *Cedrus* and *Picea*, cross-sections of the sporophyll, about the middle of the seed, showing resin ducts in both inner and outer parenchyma; in *Tsuga*, *Larix*, *Pseudotsuga*, and *Abies* they are situated in the inner parenchyma; and in *Pinus*. in the outer parenchyma only. This classification, according to the admission of the author, is "surtout artificiel."

The anatomy of the staminate strobilus has been described by AASE (1). The general tendency in the evolution of conifers to proceed from separate bract and scale to the fused bract and scale is noted; in the first group the bract and scale are separate almost to the base of the appendages, and both are about equally prominent. To this group belong *Keteleeria*, *Pseudotsuga*, species of *Abies*, and species of *Larix*.

MALE GAMETOPHYTE.—The multiplication of the cells in the male gametophyte follows the sequence characteristic of the Abietineae. There are 3 successive primary divisions; by the first and second the 2 polar ("prothallial") cells are cut off, the third resulting in the formation of the antheridial cell and the tube nucleus (figs. 1–5). This stage is the most advanced found in available material, and is believed to be the stage at which the pollen is shed. With respect to the development of the male gametophyte at the time of shedding, *Keteleeria* would resemble *Pinus* and might be contrasted with *Abies* and *Picea*. The appendage-like outgrowths of the exine and the inflation of the region between the exine and intine, caused by this growth, result in the production of wings, such as are characteristic of the Abietineae.

The mitoses involved in the development of the male gametophyte are similar to those described for *Abies* and *Picea* (**12**,**13**). In each of the first 3 mitoses the spindle fibers become oriented in such a way that they surround the polar nucleus; later they radiate from it, appearing in cross-section as tufts of fibers. This peculiarity of the mitotic figure doubtless is associated with the unequal apportionment of the cytoplasm to the resulting nuclei, an inequality which results in more favorable conditions for the more centrally placed nucleus.

In *Keteleeria* the development of the male gametophyte is not uniformly as described. Fig. 5 shows 4 nuclei medianly placed and almost equal in size. The association of such gametophytes with others whose nuclei and cells are unequal and differently placed indicates that the degree of development depends upon conditions, rather than being foreordained. When inclosed by a wall containing little cytoplasm the nucleus soon disintegrates. Fig. 4 shows 3 nuclei which are "prothallial" in nature; the third under ordinary conditions would be regarded as antheridial; in this case the nucleus corresponding in origin to the tube nucleus has taken the central position. In the struggle the nucleus which is most centrally placed gains the ascendency, the others being crowded to the wall.

MORPHOLOGY OF THE OVULATE STROBILUS.—The anatomy of the megasporophyll has been studied by AASE (1). "In *Keteleeria Fortunei* one bundle originates near the base of the gap in the strobilus cylinder and supplies the bract. It remains undivided throughout its course. Two bundles, one from each side of the gap, supply the scale; the two bundles soon unite, forming one inverted bundle, that is, its xylem faces the xylem of bract." However, in the early stages the strands connected with the 2 ovules are separate. The evidence supports the theory that the scale with its megasporangia represents a fertile bud in the axil of the bract.

The material studied shows that at the time the pollen is shed the megasporangium has reached the mother-cell stage. There is only one megaspore mother cell and it is the fourth cell from the epidermis (fig. 9), characters which still further emphasize the relation of *Keteleeria* to the Abietineae.

SIEVE TUBES.—The sieve tubes of *Keteleeria* are large, 8–10× 200–400μ, and are well differentiated. Concerning the sieve tubes of gymnosperms, DEBARY (5) states that "the oblique terminal faces are directed toward the radial planes. Sieve plates are placed in one or two longitudinal rows over the terminal faces and the whole remainder of the radial lateral face. They form roundish spots separated by high intervening portions. These spots are coarsely latticed, while in the cavities of the coarse lattice the very delicate sieve structure is seen." The appearance as seen in a surface view only has been described, and this has led to an erroneous idea of the structure. The description given by HABERLANDT (6) and DEBARY might apply to the structures as represented in fig. 6. However, transverse and tangential sections show no thickenings or depressions in the walls of the sieve tubes. The appearance of "delicate sieve structures" described for radial sections is caused by the presence of granular inclusions in protoplasmic aggregations which are situated on either side of groups of perforations in the sieve tube walls. The protoplasmic masses are connected by delicate strands which penetrate these perforations (figs. 7, 8).

The general tendency in the modification of sieve tubes from the lower to the higher vascular plants is toward an increasingly smaller number of sieve plates. First, there is a decrease in the number of walls upon which the plates occur. In some ferns each sieve tube wall contiguous with the wall of a similar cell bears sieve plates, while in most angiosperms they occur on the terminal walls only. Again, there is a tendency toward diminution in the number of plates on a given surface. In ferns (**5**, p. 180) there are several rows of plates, or they may be closely crowded together; in *Vitis* there are a number of elongated plates on the oblique septae; in cucurbits there is a single plate. In *Keteleeria* the occurrence is limited to the walls seen in radial sections and the oblique terminal walls. This is true of gymnosperms in so far as the records are available. The plates are arranged in a single interrupted series of groups. In this respect *Keteleeria* is much more advanced than *Encephalartos* (**5**, p. 181, *fig. 78*); the latter has plate groups closely distributed over the radial faces. Moreover, the plate groups are much less numerous on the radial faces in *Keteleeria* than on the oblique terminal faces. This is a further advance toward the condition in angiosperms. It seems probable that the investigation of other forms in this respect would give valuable evidence with reference to genetic relationships.

EMBRYO.—The embryo of *Keteleeria* is of considerable morphological interest; it throws light upon the polycotyledonous embryo of Coniferales, and also the meristem of the primary root shows characters heretofore unknown among gymnosperms (**2**, **7**, **8**, **9**, **10**). PIROTTA (**16**) has described the seedling.

In the embryo, as found in the mature seed, the following regions occur: cotyledons, leaf bud, and primary root. Beginning at the exterior, a cross-section of the root, taken near the central region (figs. 24, 25), shows the coleorhiza, the cortex, the region of meristematic cells and mucilage cells, and the central axis.

There is a cotyledonary tube which extends throughout approximately two-thirds of the length of the embryo. The cotyledons proper are terminal upon the cotyledonary tube, and their length is about one-sixth of that of the tube. At the base the tube is in the form of a hollow cylinder (fig. 19) above; the inner surfaces become rectangular, then star-shaped in outline (figs. 16, 17); finally, the 4 cotyledonary tips become separate (fig. 16).

Occasional seedlings of *Abies* and *Pinus* have been described (**7, 8, 9, 10**) having limited cotyledonary tubes, but no such pronounced structure as occurs in *Keteleeria* has been recorded. Although the material did not show the earlier stages, it seems evident that the situation here is similar to that existing in angiosperms (**3, 4**); that cotyledons, whether several as in Coniferales, two as in dicotyledons, or one as in monocotyledons, are all similar in origin; that the cotyledonary growth is, primarily, that which results from a meristematic ring about the leaf bud, the number of cotyledons being dependent upon the number of the loci of increased growth. In *Keteleeria* the major part of cotyledonary elongation is uniform throughout the entire ring of the growth region.

With the exception of the central axis, the regions of the primary root are similar to those of other conifers; in *Keteleeria* this region is continuous throughout, while in other conifers described it is broken by the meristematic region. It is evident that such a modification in structure is due to the nature of the meristem. Since the meristem of certain conifers, including *Keteleeria*, is being described in another paper, details may be omitted here.

The differentiation of tissues as they occur in the embryo of the mature seed is advanced beyond the stage usual for conifers (**7, 8, 9, 10**). In the primary root the first cells to become differentiated are those which later become mucilage tubes (shown in black, figs. 15–27). The cells cease to divide and become vacuolate (fig. 11); the nucleus disintegrates; the cells are greatly elongated by division and growth of the surrounding cells and become mucilaginous in content. Similar cells, except that they are much shorter, are formed in the coleorhiza. The cells of the cortex become filled with food materials, generally in the form of starch (fig. 12). The cells forming a hollow meristematic cylinder about the central axis divide in either of two planes (fig. 13). The first xylem elements, having the usual spiral thickenings of the protoxylem, become differentiated in the cotyledons; there are 4 groups of protoxylem, with 2–4 strands in each group, extending from near the tip of the cotyledon to the base of the cotyledonary tube. The protoxylem is endarch (figs. 16–20). It is significant that at this time there is no xylem present in the primary root or in the leaf bud (stem tip).

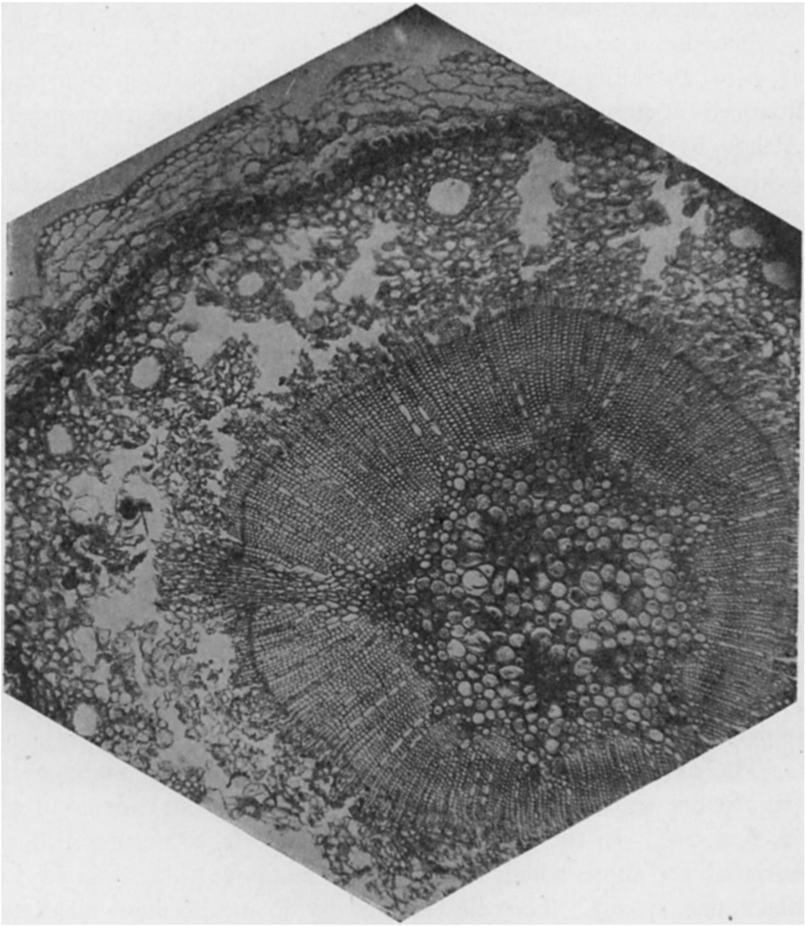

FIG. 1.—Transverse section of a branch showing epidermis, cork cambium, cortex with resin ducts, phloem, xylem, pith, and a leaf trace.

The 4 meristematic regions of the cotyledonary tube, with which the protoxylem is associated, and also the meristem of the leaf bud, connect with the hollow meristematic cylinder of the primary root. The central axis extends beyond this junction point, thereby modifying the structure generally known as the cotyledonary plate (fig. 15) (**7, 8, 9, 10**).

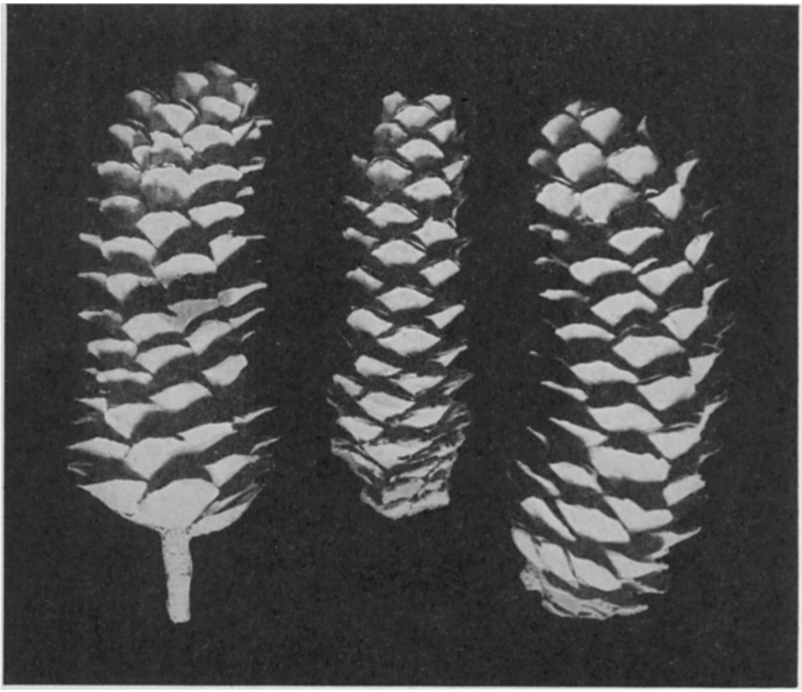

FIG. 2.—Mature ovulate cones

Summary

The following characters of the form in question warrant a genus *Keteleeria*, belonging to the Abietineae.

1. *Ovulate strobilus.*—(1) The cones are erect (text fig. 2); (2) the scales are persistent (text fig. 2); (3) the scale and bract are separate nearly to their bases (text fig. 3); (4) there is a single megaspore mother-cell (fig. 9).

2. *Staminate strobilus.*—(1) The staminate cones are borne in clusters on a fertile branch (text fig. 3); (2) there are 2 abaxial microsporangia on each sporophyll; (3) the pollen is winged (figs. 1–5).

3. *Male gametophyte.*—The pollen is shed in the 4-celled stage, consisting of 2 polar cells, the antheridial cell, and the tube nucleus (figs. 2–3).

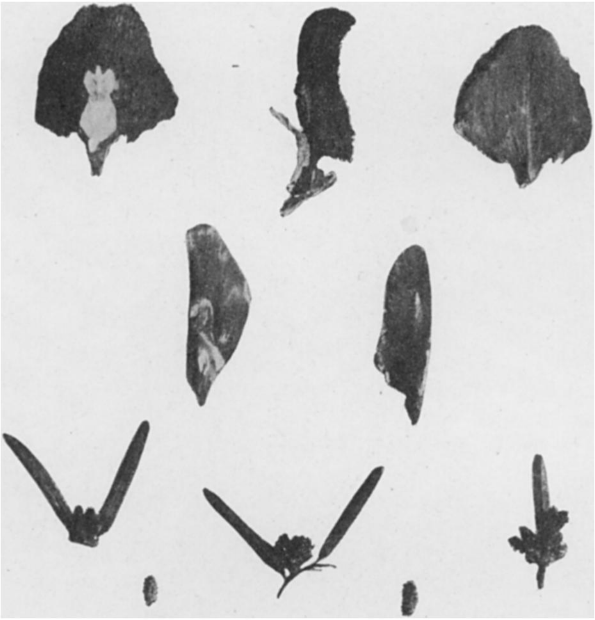

FIG. 3.—Above, megasporophylls with scale and bract separate nearly to the base; below, fertile branches bearing groups of staminate strobili; between, 2 winged seeds.

4. *Vascular anatomy.*—(1) Resin ducts do not occur in the secondary wood except as traumatic responses (text fig. 1) (**11**); (2) there are no ray tracheids nor are they "recalled by wounding" (**11**).

5. *Embryo.*—(1) There is an extensive cotyledonary tube (figs. 15–20); (2) a central axis extends throughout the primary root (fig. 15).

6. *Leaves.*—(1) The leaves are spirally arranged on ordinary branches; (2) there are 2 very closely associated vascular strands and 2 marginal resin ducts (**15**).

7. *Sieve tubes.*—These present single interrupted rows of plate groups on the radial and oblique terminal faces. Paired protoplasmic accumulations, one on either side of each plate, are connected by strands which penetrate small perforations in the intervening walls (figs. 6–8). The sieve tubes are more numerous on the oblique terminal faces, an advance toward the angiosperm condition.

8. *Cotyledonary tube.*—This is significant in connection with the theories of the origin of polycotyledony.

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EXPLANATION OF PLATES VII AND VIII

FIGS. 1–5.—Male gametophyte; ×1630.

FIG. 1.—First polar cell and second primary mitosis.

FIGS. 2, 3.—Two polar cells, antheridial cell, and tube nucleus; in fig. 3 the wall which later cuts off the antheridial cell has not yet been formed; the radiating fibers may be noted.

FIG. 4.—Three nuclei have been crowded to the wall ("prothallial cells"); tube nucleus is central.

FIG. 5.—Four medianly placed nuclei, alike in size and structure.

FIGS. 6–8.—Sieve tubes with sieve plates; ×1630.

FIG. 6.—From a longitudinal radial section.

FIG. 7.—From a longitudinal tangential section.

FIG. 8.—From a transverse section, a cell from the pith ray being shown also.

FIG. 9.—Megasporangium showing megaspore mother-cell.

FIGS. 10–14.—Cells from different regions of the embryo.

FIG. 10.—Cells from meristem of cotyledon.

FIG. 11.—Cells becoming differentiated to form mucilage tubes.

FIG. 12.—A cortical cell.

FIG. 13.—Cells from meristem of primary root.

FIG. 14.—From protoxylem of cotyledonary tube.

FIGS. 15–27.—Semidiagrammatic drawings of the embryo; ×40.

FIG. 15.—Longitudinal median section; attached numbers indicate region from which accompanying transverse sections have been taken.

FIGS. 16–27.—Transverse sections.

FIG. 16.—Cotyledons.

FIGS. 17–20.—Cotyledonary tube, showing meristematic region and protoxylem (black).

FIG. 20.—Cotyledonary tube and leaf bud.

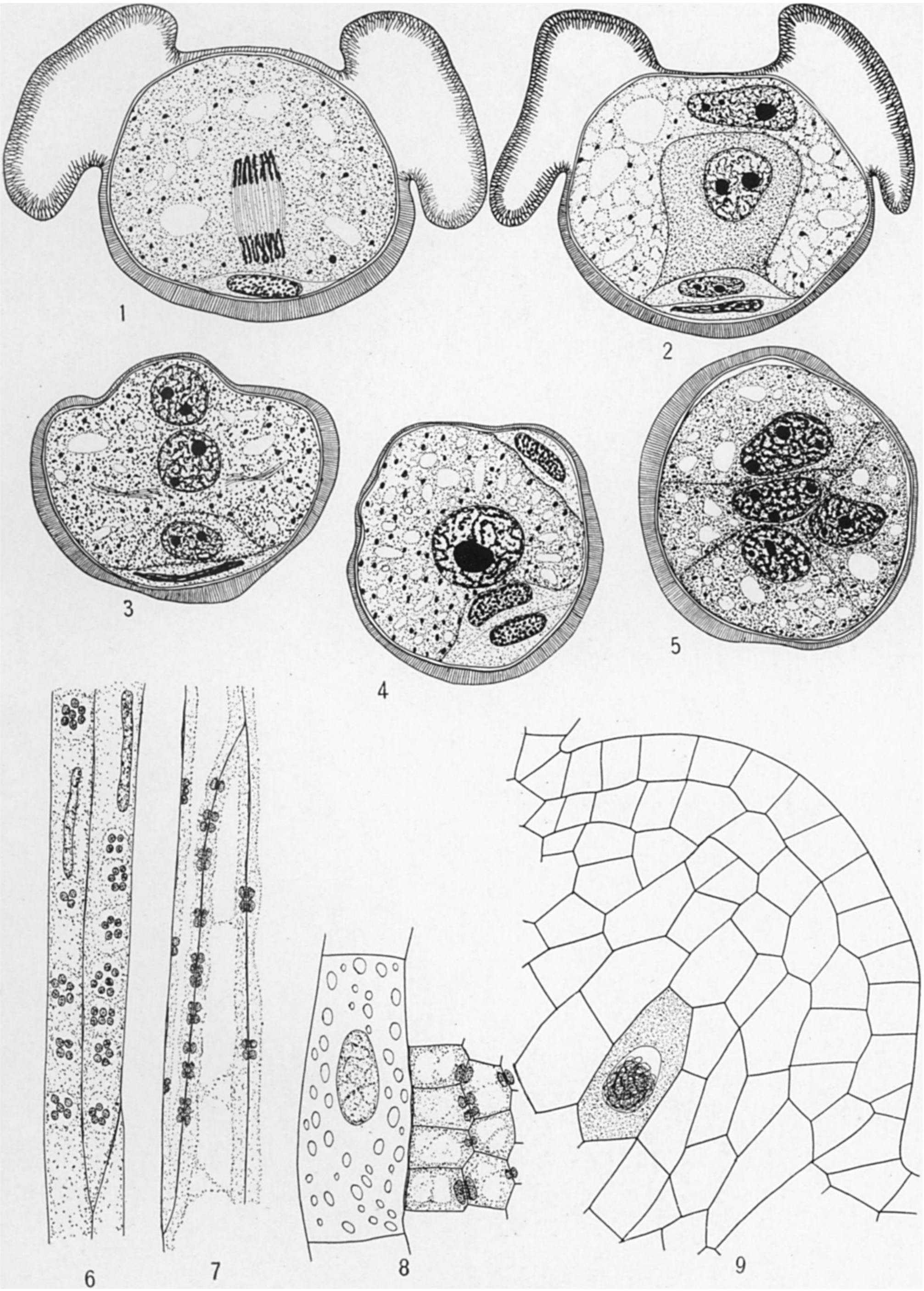
FIG. 21.—Junction of hollow meristematic cylinder of primary root and 4 meristematic regions of cotyledonary tube.

FIGS. 22, 23.—Cortex, region of meristem, and central axis.

FIGS. 24, 25.—Showing 4 regions; coleorhiza, cortex, region of meristem, and mucilage tubes; also central axis.

FIG. 26.—Section of coleorhiza, cortex, and central axis.

FIG. 27.—Section of coleorhiza and central axis.



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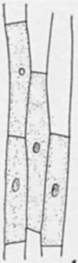

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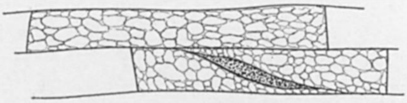

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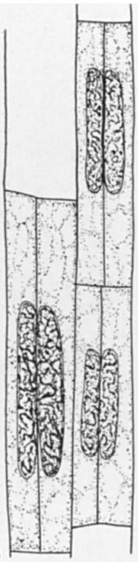

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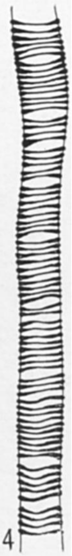

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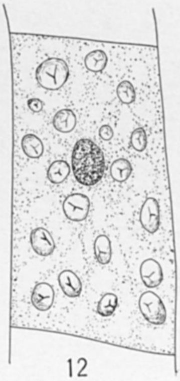

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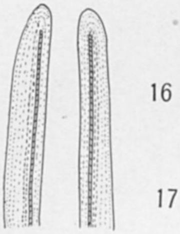

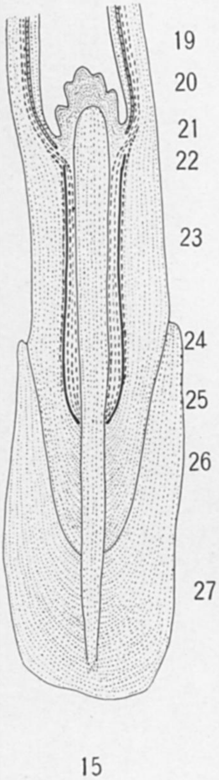

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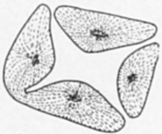

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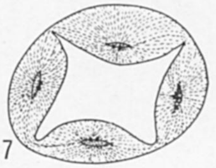

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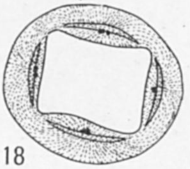

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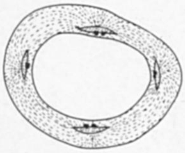

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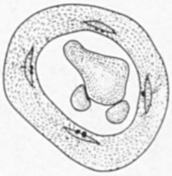

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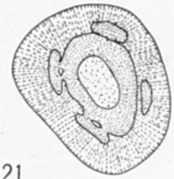

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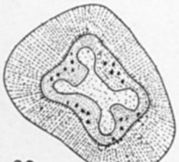

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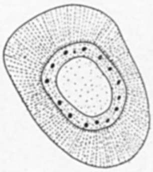

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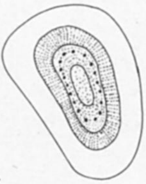

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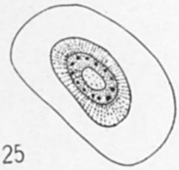

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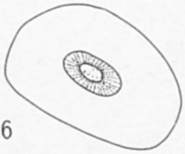

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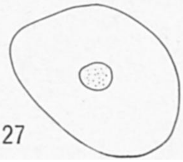

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